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A REVIEW AND CRITICISM OF SEITARO GOTO'S¹ WORK ON THE DEVELOPMENT OF *ASTERIAS PALLIDA*.

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THE study of echinoderm development has till recently remained in what may be described as a tantalizing condition. The course of the ontogeny in its main outlines has been known since the days of Johannes Müller, whose work, together with that of Professor Agassiz ('64), may be said to have given us a sketch the details of which had to be filled in. Leaving out of sight the crinoids, which are separated by a deep anatomical gulf from the other echinoderms, we had the researches of Ludwig ('82) on the development of *Asterina gibbosa*, followed by those of Semon on *Synapta digitata* (7), of Bury ('89, '95) on the pelagic larvæ generally, and of Théel ('94) on the development of *Echinocyamus pusillus*, to mention only the most important contributions to our knowledge of the subject. The general disappointing feature about the situation was that whilst there were plenty of half-worked-out problems presented, and suggestive new facts brought to light, there was an absence of any attempt to thoroughly and exhaustively examine the development of any one form, so that instead of certainties we had surmises as to the meaning and fate of larval structures.

This want I endeavored to meet some years ago by a study of the development of *Asterina gibbosa* ('96) from the blastula to the young starfish with ovaries already developed, using the most refined methods, and having at my disposal an immense amount of material. The larva of *Asterina gibbosa* is, however,

¹ Goto, Seitaro. The Metamorphosis of *Asterias pallida*, with special reference to the fate of the body cavities, *Journal of the College of Science*, vol. v. Imperial University, Tokio.

as all know, a modified one, and it was, therefore, my earnest desire that the results obtained by the examination of this form should be tested by a comparison with the development of a normal pelagic larva. And it was, therefore, with considerable pleasure that I awaited the publication of Dr. Goto's researches.

Speaking broadly, a remarkable similarity is disclosed between the two types of development. Some of Goto's figures are almost identical with those which I have already published. I shall first, therefore, sketch the general scope of the paper, and then discuss the principal points of difference between Dr. Goto and myself.

The paper commences with a description of a young bipinnaria, practically quite bilaterally symmetrical, lettered by Goto as stage *B*, the stages considered in the paper being denoted *B, C, D, E, F, G, H*. [I assume, although Dr. Goto does not say so, that the lettering has been chosen to correspond as far as possible with the lettering of the stages of *Asterina gibbosa* given by me; stages *E, F, G*, and *H* appear to be identical in the two cases, and unless this were so, I utterly fail to grasp why Dr. Goto calls the first stage *B*. It is to be desired that this should be explicitly stated, since it is undesirable to introduce an independent lettering with every new species examined.] The changes in external form are then carefully explained; the plane of the developing disk of the starfish is at first parallel to the sagittal plane of the larva; but as development proceeds it is shifted backwards until it occupies the posterior pole of the larva, and is then perpendicular to both the sagittal and frontal planes — so that the direction right to left in the larva is parallel to the disk, as well as the direction dorsal to ventral.

As development proceeds, three "brachiolar" arms are developed on the præoral lobe surrounding a thickened patch of ectoderm, and so the bipinnaria becomes a brachiolaria. Dr. Goto was unable to observe any fixation during the metamorphosis, such as has been seen by Bury ('95) in the case of *Asterias rubens*, and by myself in *Asterina gibbosa* ('96).

As in the case of *Asterina gibbosa*, and contrary to what was believed to take place in the case of bipinnaria, both the larval œsophagus and the larval rectum atrophy; — the præoral lobe

gradually shrinks, and thus the metamorphosis is complete. It is interesting to note that, according to Goto, the permanent œsophagus is fashioned out of the endodermal stump of the larval one.

The fate of the cœlomic cavities next claims Dr. Goto's attention. Originally represented by two completely separated right and left sacs, these spaces have at the period of the first stage studied completely fused in the region of the præoral lobe. The left one is sharply constricted into anterior and posterior portions, and the right undergoes a similar constriction somewhat later. In *Asterina gibbosa*, it will be remembered, there is not only constriction, but also complete separation into two parts in the case of both cavities. The left posterior cœlom assumes a U-shaped form, sending out dorsal and ventral horns. A portion of the right posterior enterocœle is cut off from the rest and forms a closed sac, the "epigastric" cœlom subsequently occupying an aboral position in the young starfish. The remainder of the right posterior cœlom fuses with the left posterior cœlom. The anterior cœlom becomes completely cut off from the posterior cœlomic sacs, and with the diminishing præoral lobe becomes largely obliterated, a portion persisting, however, as the axial sinus. In the septum dividing it from the left posterior cœlom, the stone canal is formed as a groove; this accordingly takes place long after the formation of the pore canal.

Simultaneously with the diminution in size of the anterior cœlom, the watervascular rudiment, present from the first stage as a posterior swelling on the anterior cœlom, becomes completely separated from the axial sinus, the only communication remaining being that *via* the stone canal.

The axial sinus gives off a diverticulum, which forms the dorsal sac of Bury — a structure denominated by me the right hydrocœle. According to Goto, it originates on the left side of the larva.

A peculiar diverticulum of the left posterior cœlom, mistaken by Ludwig ('82) for a rudiment of the "heart," gives rise to a space surrounding the adult œsophagus, and is named by Goto pericœsophageal cœlom. It was called by me "oral cœlom."

Lastly, Dr. Goto discusses cavities of "mesenchymatous" origin. Under this heading he includes the peribranchial cavities surrounding the dermal gills, or papulæ, and the radial perihæmal canals, together with the outer perihæmal ring. These spaces, according to him, originate entirely independently of the cœlom by the hollowing out of originally solid masses of mesenchyme cells. The inner perihæmal ring, on the contrary, is an outgrowth of the axial sinus.

Seitaro Goto confirms my statements as to the total want of homology between the aboral poles of the asteroid and crinoid, the origin of the axial sinus and the stone canal, and the persistence of a communication between them, and the origin of the pericœsophageal cœlom and of the inner perihæmal ring. On the other hand, the results of my investigations, which seemed to me the most interesting and important, namely, the primitive segmentation of the cœlom, the existence of a right watervascular rudiment or hydrocœle, the presence of a permanently fixed stage in the ontogeny, and the denial of the existence of any spaces of mesenchymatous origin, are not confirmed by Goto.

It will conduce to brevity and clearness if I state shortly and definitely my position with regard to this discordance in opinion. I am convinced, from the general outline given by Goto, that the development of *Asterina gibbosa* and the development of *Asterias pallida* are in all essential points identical in character. I have submitted my own sections to reëxamination, after reading Dr. Goto's paper, and find them decisive; and I find enough imperfection in Dr. Goto's methods to more than account for all the differences between us.

My work was based on hundreds of complete series of sections of larvæ fixed by a method which was selected, after a long series of trials, as preserving the outlines of the organs with the sharpness of the lines in a steel engraving. I find no evidence whatever that Dr. Goto examined anything comparable to the number of larvæ seen by me, and the method of preservation adopted by him is one of the worst suited for the purpose.

I do not question the accuracy of Dr. Goto's statement as

to the backward displacement of the disk of the young starfish ; but I regard the coincidence between the sagittal plane of the larva and the vertical plane drawn through the madreporic pore and the mouth of the adult as an accidental agreement of no deep significance. The backward movement of the disk does not take place to anything like the same extent in *Asterina gibbosa*. It remains true there, in spite of Dr. Goto's denial, that right to left in the larva is nearly dorsal to ventral in the adult. Sections orientated parallel to the frontal larval plane have given longitudinal sections of the stone canal which would be impossible were the relations of adult and larval planes such as described by Dr. Goto.

With regard to the absence of the fixed stage, it is to be regretted that Dr. Goto has given us no information as to how he obtained his larvæ — whether they were reared from the egg, or whether they were obtained by the use of the tow net. Ludwig failed to find the fixed stage in *Asterina gibbosa*, probably because the larvæ were not provided with a suitable substratum ; and if Dr. Goto fished his metamorphosing larvæ out of the sea, it is quite conceivable that the time when fixation could occur was past, or that no suitable basis was provided for fixation. Glass is assuredly not such a substance ; I never saw an *Asterina* larva fixed to glass ; and it is surely not probable that the brachiolarian arms are developed for no purpose.

I come now to what I regard as one of the most serious points of difference, namely, the meaning of the sac called by me the right hydrocœle. In support of this position, I gave not only a clear account of its appearance unequivocally on the right side of the larvæ, but I also described a number of cases where exceptionally the sac had undergone further development, and produced lobes similar to those formed by the left hydrocœle. Now, Goto has not seen the origin of the structure at all, this occurring at a stage considerably previous to any which he has figured, and his statements as to its later connection with the axial sinus are entirely due to the preservation of his larvæ. Many times in the earlier portion of my work was I tempted to make the same statement before I found out that corrosive sublimate was unsuited for the preservation of these larvæ.

The account given by Goto of the segmentation of the body cavity is also most unsatisfactory, and raises the suspicion of many stages having been missed out. At any rate, he gives no ground whatever for his belief that the "epigastric" coelom is only a portion of the right posterior coelom, for he has not shown how he can define the latter space. The stages he describes recall the period in *Asterina* development when the segmentation of the coelom, after being formed, has to some extent broken down; and as it is in the highest degree improbable that *Asterina gibbosa* has a more circuitous development than *Asterias pallida*, a reëxamination of this point, based on more abundant material, would probably put a different complexion on the affair.

The criticisms made above with reference to the right hydrocoele apply with tenfold greater force to the origin of the perihæmal cavities. These originate long before Seitaro Goto saw the first trace of them. As to their origin from the coelom, not the slightest doubt can exist in the mind of any one who has seen a properly prepared section of a metamorphosing *Asterina* larva. I have figured one of these rudiments under the magnification obtained by a Leitz immersion, putting in the outline of every cell, in Fig. 139 of my paper ('96), and the communication with the coelom is no dubious slit, but a broad opening. This opening surprisingly soon closes up, and in later stages one could imagine the space to be of mesenchymatous origin, if one had not seen the earlier stages.

I may say definitely that I am very sceptical as to the mesenchymatous origin of any cavity. The mesenchyme is primarily a series of amœbocytes floating in a cavity, which answers retrospectively to the jelly of coelenterata, and prospectively to the hæmocœle of the higher animals. That these amœbocytes should first coalesce, and then hollow out to form a cavity within a cavity, seems exceedingly improbable, especially when one remembers how easy it is by missing out stages to lose entire sight of the genetic connections of two organs.

In conclusion, I must remark that Seitaro Goto's work is not suited to solve the problems he attacks. Echinoderm larvæ are most difficult objects to handle. Bury himself ('95)

remarks that his early results are unreliable, because he had not imbedded in celloidin, — a statement with which I fully concur, — and it never seems to have occurred to Goto to use celloidin. Osmic acid, again, is the only reagent which will preserve the delicate epithelia so that one can be sure of their actual extent. And Goto used corrosive sublimate mixed with glycerine, an absolutely fatal compound for histology. Again, so far as one can judge, a most insufficient amount of material was used. And there is no subject on which it is so easy to go fatally wrong as organogeny, except an unbroken series of stages be obtained.

We have now reached a stage in embryological research where progress can only be made by the most refined methods, and by the exercise of abundant caution. The day of breaking ground is past. Of course the method of thorough exploration by sections is slow and laborious, and in these days of impatience for quick results it is apt to be shirked; but in my opinion it is the only one which will lead us any farther in our acquaintance with developmental processes.

MONTREAL, October 22, 1898.

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